TAXONOMY OF THE FUNGI FORMING ENDOMYCORRHIZAE

A. Vesicular-arbuscular Mycorrhizal Fungi (Endogonales)

James M. Trappe and N. C. Schenck

INTRODUCTION

Beniamino Peyronel (8, 9) in 1923 was the first to recognize that the vesicular-arbuscular mycorrhizal (VAM) fungi were members of the Endogonales, rather than chytrids, Pythium spp., or other fungi as suggested by earlier workers. Peyronel's discovery followed the revision of the Endogonaceae by Thaxter (11), who had not realized the mycorrhizal involvement of the family. The ensuing three decades witnessed little activity in taxonomic study of these fungi, because they were so rarely encountered. Gerdemann and Nicolson (5) then developed procedures for collecting spores from soil and described new species found by their techniques (7). The family was monographed in 1974 with segregation of the genus Endogone into seven genera (6); since then, steady discovery and publication of new taxa has added a genus and nearly doubled the number of species (13).

We now realize that the Endogonaceae are among the more common and widely distributed of the soil-borne fungi, and much new information about them has been obtained. Still, much mystery remains, and we continue developing hypotheses to clarify taxonomic concepts. To do this, similar individuals are grouped into species, a straightforward process for very distinctive groupings but an ambiguous one when extremely different spores are linked by a series of intergrading forms. The latter case occurs with some of the very common VAM fungi, e.g. Glomus microsporum-G. fasciculatum-G. macrocarpum. Unhappily, presently used criteria are inadequate to fix neat boundaries between intergrading taxa. Some of these complexes may be resolved by new techniques, but we must also be prepared to acknowledge that some may prove unresolvable in taxonomic terms. Nonetheless, we must continue to try, because nomenclature that reflects reality in speciation is necessary to scientific communication. An accurate species name permits us to make predictions about a fungus, and the literature now abounds with evidence that different VAM fungi can interact with hosts and environment in very different ways. Accurate species designations are required to avert chaos in VAM research.

The VAM Genera and Their Defining Characters

The Endogonales (Zygomycotina) as presently conceived consists of a single family, the Endogonaceae. The genera are separated at the first level on the manner of spore formation, as inferred from the morphology of spores and spore-bearing structures. Within the chlamydosporic taxa, further generic separation is based on sporocarp morphology. The type genus, Endogone, forms zygospores but is not known to produce VA mycorrhizae. Acaulospora, Entrophospora, Gigaspora, Glaziella, Glomus, and Sclerocystis have not been demonstrated to form zygospores and contain either proven or presumed VAM species.

Two additional genera have been tentatively placed in the Endogonales in the past. Modicella forms only sporangia and appears to be saprobic; we exclude it from the Endogonales, because it fits more comfortably with the Mortierellaceae (Mucorales). Complexipes is based on chlamydospores formed by certain Discomycetes, probably in the family Pyronemataceae (4).

Two kinds of spores are hypothesized for the VAM genera on the basis of spore morphology. No data are available on the cytology or sexual vs. asexual processes involved in formation of these spores; when such data become available, our concepts may change in some cases. The spores of Acaulospora, Entrophospora, and Gigaspora have been termed azygospores, i.e. parthenogenic zygospores, because they rather resemble the zygospores of Endogone spp., but no sexual orgin

has been observed (2, 6). The spores of Glaziella, Glomus, and Sclerocystis are regarded as chlamydospores, i.e., specialized asexual resting cells.

The distinctive combination of characters that defines each VAM genus is summarized below. Each genus has been described in detail by Gerdemann and Trappe (6); this publication, out of print for several years, in now again available from the U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station, 809 NE 6th Ave, Portland, OR 97232.

We avoid use of the term "vesicle", because in the VAM literature it has been applied to four quite different kinds of unrelated structures. To minimize confusion, we prefer to reserve the term only for the vesicles that form within roots as part of the vesicular-arbuscular mycorrhiza.

Acaulospora, (Fig. 1; Plate 1A).-- Azygospores bud laterally from the funnel-shaped stalk of a large, inflated hyphal terminus (6). By spore maturity, the funnel-stalked cell collapses; its amorphous remnants may cling to the spore but often detach to leave the spore with no sign of its origin except for a small pore with an inconspicuous rim. The spores are borne singly in soil or sometimes within roots (1, 6). Keys to the eight species presently known are provided by Trappe (13) and Walker and Trappe (15).

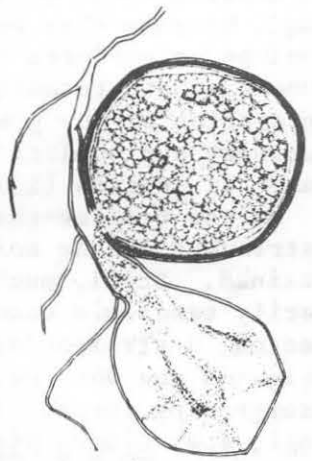

Fig. 1. Acaulospora laevis (cross section, x 100)

Entrophospora (Plate 1E)-- Azygospores are formed within the funnel-shaped stalk of a large, inflated hyphal terminus (2). As the spore enlarges, the stalk expands to produce a second swelling below the inflated hyphal terminus. The end result is a peanut or dumbbell-shaped cell with the spore in the basal, swollen part. Meanwhile, the walls of the spore-enclosing structure become greatly thickened. Ultimately the terminal swelling collapses and detaches, leaving the spore enclosed by the thick, appressed wall of the former stalk of the inflated hyphal terminus. The spores are borne singly in soil. Only one species has been described (2), but a second has been recently discovered (Schenck, unpublished data).

Gigaspora (Fig, 2: Plate 1B,C).--Azygospores bud from the bulbous, suspensor-like tip of a hypha. As the spore expands and approaches maturation, one to several septa form below the suspensor-like bulb, which usually remains attached to the spore and produces one to several, narrow, out-growing hyphae (6). The uppermost of these grows to the lower spore surface, where it apparently terminates without fusing with the spore. The spores are borne singly in soil. Keys to most of the 17 presently recognized species are provided by Trappe (13).

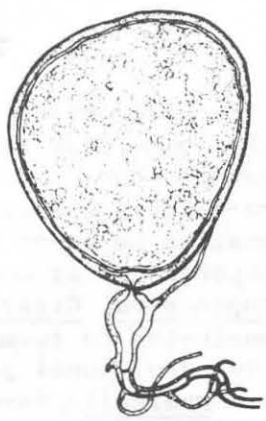

Fig. 2. Gigaspora calospora (cross-section, x 200)

Glaziella-- Chlamydospores, formed singly at hyphal tips, are scattered in the walls of large (1.5-5 cm diam), hollow, bright orange to red sporocarps (11). Known only from tropical lowlands, especially near the coast, this unique fungus forms sporocarps in the soil, but expansion of the sporocarps lifts them out of the soil. Often they are found lying loose on the ground. They float freely in water and may have evolved this sporocarp form for water transport by ocean currents. Only one species is presently recognized.

Glomus (Figs 3, 4; Plate 1F-H; Plate 2A,B). --Chlamydospores form at a hyphal tip, usually one per tip, but in G. fuegianum several spores emerge from a swollen hyphal tip (6, 11). By maturity, the spore contents are separated from the attached hypha by a septum (Fig.3) or by occlusion with deposits of wall material (Fig. 4). Two or more hyphae may be attached to spores of some species. Care must be taken not to confuse a basal protrusion of a Glomus spore (Fig. 3) with the suspensor-like bulb of Gigaspora spp. (Fig. 2). Spores of most Glomus species are borne singly in soil, but some of the same species may also form them in the cortex of roots (6, 10) or in sporocarps (6). A few species are known only from sporocarps. Most sporocarps of Glomus spp. are nonorganized conglomerations of spores. In G.radiatum the spores are randomly positioned but radiate from the sporocarp base, those nearest the base being the most mature. Most of the more than 40 species presently recognized are in Trappe's keys (13).

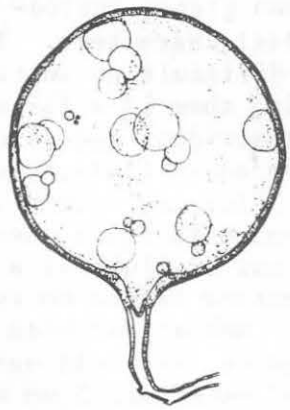

Fig. 3. Glomus mosseae (cross-section, x 200)

Sclerocystis (Fig 5; Plate 2C,D).-- Chlamydospores form in sporocarps as a single, crowded layer of erect spores that surrounds the sides and top of a spore-free, central mass of tightly interwoven hyphae. The sporocarps may be borne singly in soil or fused together in crusts on organic debris or moss at the soil surface (the latter case appears to occur only in the wet tropics or in humid glasshouse conditions). All presently known species are included in the key by Trappe (13).

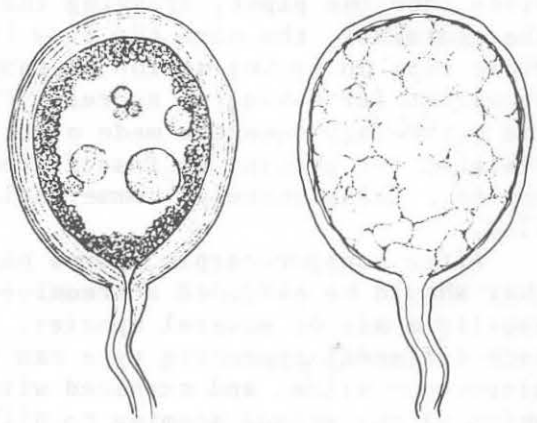

Fig. 4. Glomus fasciculatum, right spore young, left mature with laminated wall (cross-section, x 500).

Characters Important in Species Identification

Methods of observation.-- Firm identifications usually require numerous spores, although a single spore in prime condition can often be identified to species. To determine reaction to reagent or stains or to define variability in size, color, degree of maturation, etc., many spores from a single collection are needed. We like to have at least 20 and prefer 50 or more. Moreover, it is useful to crush spores to define wall structure; once crushed, a spore has limited value for other uses. Voucher collections for herbarium deposit increase in usefulness with increasing numbers of spores, and type collections of new taxa should contain as many spores as practicable.

Microscope mounts of spores from sporocarps are easy to make if the sporocarps are large enough to manipulate by hand. Cut the sporocarp in half with a razor blade along the axis of the point of sporocarp attachment, when such a point can be found. Intact spores can usually be teased from the exposed gleba directly onto

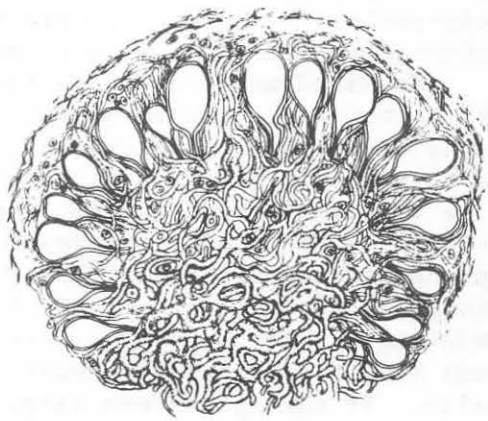

Fig. 5. Sclerocystis coremioides sporocarp (cross-section, x 100)

a microscope slide. Alternatively, thin slices of gleba can be cut from the exposed gleba; include the sporocarp surface in the slices for evaluation of peridial characters. Tiny sporocarps, such as those of Sclerocystis spp., are more difficult to section. With patience, decent sections can be obtained by holding them in a forceps and cutting razor blade slices under a stereomicroscope.

Individual spores can be picked up in a number of ways. If they are not suspended in fluid, touch them with the side of a dissecting needle (moisten the needle for dry spores), and they will cling to it. More often, the spores are suspended in fluid when they are to be manipulated. A simple tool for picking them out of fluid is a dissecting spade. To make a spade, heat the tip of a dissecting needle to redness, then hammer it flat. Make the tip especially thin. Reheat and bend the tip in a slight upward curve. Then reheat again and plunge it into cold water to temper the steel. Individual spores can be picked out of water ca. 5 mm deep by slipping the spade under them and lifting them (break them through the water surface tension abruptly). The technique is somewhat tricky but easily mastered with a little practice. In experienced hands it is very quick. A small-bore glass pipet is an easy alternative, (R. Ames, personal communication). Place a finger over the top hole of the pipet, then lower it into the water and over the spore. Release the finger, and the water rises into the pipet, dragging the spore with it. The higher the water level in the container, the more the flow into the pipet when the finger is released. Pipet tips on spring-action or thumbscrew suction control syringes are also excellent for taking up spores. C. Walker (personal communication) recommends the entomology tweezers made of thin gauge, springy stainless steel. These are designed for picking up insect specimens without damage and are excellent for spores. Unfortunately, commercial sources of these tweezers are difficult to find.

After nonsporocarpic spores have been extracted from soil (see Chapter 3), they should be examined stereomicroscopically. Collections from the field are usually a mix of several species. Several representive spores or sporocarps of each different appearing type can then be removed, placed on a drop of water on a microscope slide, and examined with a compound microscope. One can usually judge which of the groups seeming to differ by stereomicroscopy are indeed different taxa and which are simply variants or developmental stages of a single taxon. For example, some nearly colorless spores may prove to be young, thin-walled specimens of the same taxon that is also present as more colored, thick-walled, mature spores. Dull-surfaced spores may be senescent, with surfaces roughened by microbial degradation but otherwise clearly the same as similarly colored but bright and shiny spores. After these initial spores are evaluated, one can return to the steromicroscope and sort the rest of the spores, putting each type in a separate container of water (watch glasses or small evaporating dishes are appropriate if the spores are to be examined immediately; screw cap vials for storage in a refrigerator if examination will be delayed).

Standard mounting media for determining species can be water, lactoglycerine, or lactophenol. Avoid 3% KOH, a standard medium in mycology, because it induces unnatural swelling of the walls of some Endogonales. Two drops of the mounting medium can be put on a microscope slide, one drop near one end of the slide and one in the middle. A drop of Melzer's reagent can be put on the other end of the slide. A dozen or so spores can be selected from one of the sorted batches and placed in the drops of standard medium in the middle of the slide; attempt to include the smallest and the largest spores as judged by stereomicroscopic viewing. Three or four spores can be put into the end drop of standard medium and into the Melzer's reagent. Each drop is covered with a 20 x 20 mm cover slip. If the spores are exceptionally large, two or three drops may be needed to fill the space between the slide and the cover slip. The spores in the end spot of standard medium are percussion-crushed by gently bouncing a pencil, eraser side down, on the top of the cover slip. Avoid an excess of medium in the spot to be flattened by percussion crushing.

With these three mounts on a single slide, one can observe all the characters needed to key out the species. This can be done directly by starting in the key

and observing each character in turn as called for by the key. Or, the spore characters can be recorded in full and then keyed from the notes. In the latter case, retain the slide in case the key calls for something not recorded.

Staining spores in cotton blue-lactophenol (or lactoglycerine) sometimes reveals spore structures difficult to see clearly in unstained specimens. To stain quickly, place several spores in a drop of cotton blue on a slide, add a glass (not plastic) cover slip, and flame to boiling by holding a lighted paper match under the cotton blue with the tip of the flame 1 cm below the slide. Remove the heat as soon as the medium begins to boil. When it reaches boiling, the mount may spit tiny droplets of cotton blue, so hold at arm's length when applying the heat. If the mount need not be examined for a day or so after preparation, the spores will usually stain satisfactorily in the interim without heating. After an extended period in cotton blue, most spores stain so intensely that structural details are obscured.

Sporocarps.-- These may range from rather large (Glaziella, some Glomus spp.--Plate 1F) to less than 0.5 mm in diam (some Glomus and Sclerocystis spp.--Fig. 4; Plate 2C,D). Important characters in addition to size are sporocarp surface color; nature of the peridium, ranging from absent to a loose tangle of surface hyphae, a tightly interwoven cutis, or a pubescence of erect hyphal tips; color and organization of the interior; and arrangement of spores. It is important to cut sporocarps along the axis of the point of sporocarp attachment, when such a point can be found, to accurately determine interior structure and spore arrangement.

Spore dimensions.--Spores are measured by use of an ocular micrometer in the eyepiece of a compound microscope. Spore length is along the axis of the point of spore attachment and width is at angles to that attachment. The two measurements are customarily presented length first, width second, but inconsistancies are common in the older literature and continue to appear occasionally. If spores are ornamented, measurements excluding the ornamentation are customarily recorded separately from the height of the ornamentation. Spore dimensions within a species and even within a single sievings can vary considerably, the more so with the larger spored species. Hence the range of dimensions should be recorded. Occasional spores sometimes exceed the dimensional range of the great majority of spores. These exceptional cases are recorded in parentheses, e.g. (26-) 30-55 (-61) µm.

Hyphal mantles.--Spores of some Glomus spp. are wrapped in interwoven hyphae. In some cases the mantles separate readily, but often the mantles are tightly adherent. This is an important character for species identification but it complicates study of the spore walls and attachment. Spores will pop out of nonadherent mantles when crushed by pencil percussion. If mantles adhere, more forceful percussion can be used to break spores apart, so that at least the broken ends of the walls can be observed. In either case, the hyphal attachment is difficult to find. One must then work patiently with large numbers of spores in hopes of finding hyphal attachments. Young spores in early stages of mantle development sometimes offer the best chance.

Spore ornamentation.--A distinct surface ornamentation delights the identifier of species of Endogonales, not only because of the beauty often displayed but also because it markedly narrows the choice of species. Ornamentation may be spines, warts, wrinkles, pits, a reticulum, etc., or a combination of two or more of these. The pattern, height, size of the elements (e.g. warts or spines) can all be diagnostically useful.

Biological or physical-chemical weathering can produce a dull roughening on the surface of old spores that were shiny-smooth when younger. The degradation can be mistaken for ornamentation, although it tends to be amorphous and erratic rather than distinctive or patterned. Weathered spores generally occur among spores in prime condition, and the two can generally be equated by characters other than surface if the collection contains numerous spores.

Spore walls.-- Walls are extremely important in taxonomy of the VAM fungi, but they can be confusing. All spores begin with thin walls (Fig. 4). As the spores mature, the walls may thicken to only 1 µm or so in some species or to

more than 20 µm in others. Furthermore, the walls of some species differentiate into two to several distinct layers, and in a few of these species the outermost layer may flake away or erode just as inner layers are differentiating. Acaulospora and Gigaspora species commonly form one to several separable membranes within the primary spore wall. To compound the problem, the thickening of walls in some collections of Glomus spp. proceeds uniformily but in other collections is apparently intermittent. The latter circumstance results in a series of successively fused deposits which have been termed laminations (Fig. 4). When present in a spore wall, laminations are usually indistinct or discontinuous, but occasionally they appear as distinct and uniform as annual rings in a tree.

Assessment of spore wall structure is stepwise. First, intact spores should be examined with the high-dry microscope objective focused at optical cross section. Then, unless spores are opaque or extremely large, switch to oil immersion. The thickness, color, and any other distinctive feature should be recorded for each differentiated layer (but this generally is not useful for individual, fused laminations). A drawing is useful for complex differentiated wall layering. Repeat the steps with crushed spores, noting which layers are separable and differences from the observations of intact spores. Use the oil immersion objective. Then examine spores mounted in Melzer's reagent with the high-dry objective, specially noting distinctive color reactions of each layer. Before switching to oil immersion, crush the spores in Melzer's regent by percussion, then re-examine with the high-dry objective. If any distinctive color reaction is seen, examine with the oil immersion objective.

By these techniques, even the most complex spore walls can usually be accurately evaluated, although in some cases considerable time and patience is needed. If one is uncertain whether the specimens have truly differentiated wall layers or fused laminations of a single wall, the edge of the fracture of crushed spores will nearly always resolve the issue. Nonseparable differentiated layers will often break at slightly different spots, so the fracture edge will show angular discontinuities from one layer to the next (examine several spores). A single wall with fused laminations, in contrast, will generally fracture cleanly with no discontinuities between laminations.

Artifacts of spore wall structure sometimes result from parasitism. The invasion of a parasite through the spore wall, for example, can produce a pore; a single spore may have many such pores. These are random or erratic rather than in the regular pattern that would be expected if the pore were produced by the spore itself. Often the spore reacts to such parasitic penetrations by depositing inner wall material over them. The parasite then invades further, and the spore deposits additional wall material around it. This results in pored stalagmite-like growths from the inner surface of the spore wall.

Spore contents.-- Color of spore contents is occasionally useful in species identification. The spores of Glomus convolutum, for example, are filled with deep yellow oil globules, the source of the yellow color of the sporocarps (Plate IG). Spores of most species, however, have colorless contents. The form of contents of fresh, mature spores tends to differ between azygosporic taxa, which are filled with nearly uniform, small oil globules (Figs. 1, 2) and chlamydosporic taxa, which contain a wide range of oil globule sizes (Figs. 3, 4). Some chlamydospores, however, have "azygosporic-type" oil globules. With drying or freezing, the many oil globules within spores often coalesce into a single, large globule. The contents of senescing spores sometimes become crystalline or amorphous. Because of these variations, spore contents have limited taxonomic use. An exception is Glomus radiatum, which fills its spores with hyphae by maturity (6).

Hyphal attachments.-- The importance of hyphal attachment characters for generic determination has been outlined earlier in this chapter, but hyphal attachments are also useful at the species level. In Gigaspora, for example, the suspensor-like bulb is the same color as the spore in most species but a different color from the spore in a few species. Glomus species separate into two major categories of hyphal attachment closure; those closed by a septum (Fig.

3) vs those occluded by thickening of the spore wall (Fig. 4, Plate 2B). Some Glomus species are more readily differentiated by the hyphal attachment than by the spores themselves. For example, Glomus etunicatum spores sometimes resemble those of G. caledonicum, other times those of G. fasciculatum or G. macrocarpum. The hyphal attachment of G. etunicatum, however, is closed by a septum and is 5-8 um in diam, and the attached hypha is colorless, with only slightly thickened walls. In contrast, tne other three Glomus spp. have hyphal attachments occluded by spore wall thickening and routinely 10-20 µm in diam, and the attached hypha is pigmented and very thick-walled. Some Glomus species regularly have two or more attached hyphae. These may ultimately prove to be sexual spores, but for lack of evidence on sexuality and for their morphological similarity to chlamydospores of other Glomus spp., they are presently retained in Glomus.

The difference between the attachment of Gigaspora spp. and Glomus mosseae needs special mention, because many beginners confuse them. Compare figures 2 and 3. Gigaspora spp. bud from a suspensor-like bulb; the point of attachment is strikingly constricted, and a narrow pore penetrates from the bulb through the outer spore wall. Glomus mosseae has a basal protrusion of the spore itself, typically funnel-shaped as shown in figure 3 but sometimes cylindric; the point of attachment is not constricted and is closed by a septum with no visible pore.

Detailed descriptions of hyphal attachments and the attached hyphae have sometimes been neglected in the past, but now the characters of these structures are known to often have diagnostic value. Redescriptions and descriptions of new taxa should detail the diameter of the attachment and the nature of its closure. Descriptions of attached hyphae should include diameter at attachment plus changes in diameter below the attachment, color, wall thickness and layering, septation, presence of subsidiary hyphae or hyphal branching, and any other distinctive features observed.

Soil-borne auxiliary cells of Gigaspora spp.-- Hyphae of Gigaspora species produce fine, coiled hyphae terminated with small, specialized cells or clusters of cells (Plate 1D) termed "soil-borne vesicles" or "extramatrical vesicles" in the past. The function of these cells is unknown. To avoid confusion with other uses of "vesicle" in VAM terminology, we prefer to call these structures "soil-borne auxiliary cells" until a more specific, functional term can be coined. Gigaspora spp. differ in producing auxiliary cells singly vs in clusters of a few vs clusters of many. Young auxiliary cells are smooth and hyaline to subhyaline but when fully developed are mostly ornamented with knobs, warts, spines, or coralloid projections and, in some species, become brown walled. Gigaspora species can generally be identified by spore characters alone, but retrieval of auxiliary cells for confirmation of identification should always be attempted.

Manner of spore germination.-- Germination has been observed for only a relatively few species of Endogonales but is known to differ between species of a given genus. The inner and outer spore walls of some azygosporic species separate to form a cavity that becomes compartmentalized by cross walls. Each compartment may produce a germ tube through the outer spore wall. Other azygosporic species may simply germinate through the spore wall with no inner compartmentalization. Chlamydosporic species seem mostly to extend a germ tube from the hyphal attachment through the attached hypha, but a few species have been observed to germinate through the spore wall. As more data accumulate, the manner of spore germination will doubtless prove useful in reassessing genera and subgenera. It is useful in identifying taxa only when germinated spores are available.

Histochemical reactions.-- Histochemical reactions have assumed prominence in taxonomy of ectomycorrhizal fungi, but little has been attempted so far with VAM fungi. Melzer's reagent produces diagnostically useful reactions with some taxa, e.g. an intense reddening of inner membranes of Acaulospora spp. or presence of green to black granules and stains in hyphae of Glomus convolutum. Other reagents need to be tried, but at present we have no basis for suggesting which ones other than those which have proven useful with other groups of fungi.

Preservation of Voucher Collections

Type collections of new taxa are always deposited in a publically accessible herbarium, but we cannot emphasize too strongly the critical importance of similarly depositing voucher collections of VAM fungi collected in the field, grown in pot cultures, or used in experiments. We urge careful reading of the paper by Ammirati (3) on this subject.

Herbarium specimens of sporocarps can be air-dried and deposited in envelopes or packets. Tiny sporocarps or nonsporocarpic spores and hyphae are customarily preserved in vials of lactophenol, which will last indefinitely in tightly closed vials sealed with parawax and will prevent growth of contaminants. Unfortunately, spores sometimes change color with time in lactophenol. L-drying offers an excellent alternative for suitably equipped laboratories (12). As many spores as practicable should be deposited for each collection, but few spores are preferable to none. Auxiliary cells of Gigaspora species should be included with Gigaspora collections when available.

It is also helpful to include microscope slides of spores along with preserved specimens. One convenient method for preparing slides in polyvinyl alcohol lactophenol (PVL) is described by Walker (14). Dissolve 15 ml polyvinyl alcohol granules (50-75% hydrolyzed: 20-25 centipoise viscosity when in 4% aqueous solution at 20%°C) in 100 ml distilled water in a water bath at 80°C. This may take several days with occasional stirring. The resulting stock solution keeps well in dark bottles. To make PVL mounting medium, mix 56 parts of the stock solution with 22 parts each of lactic acid and liquid phenol. Fresh, rehydrated, or dry spores are placed on a microscope slide and covered with a drop of PVL. Arrange the spores at the center of the PVL with a needle and put on a glass cover slip. If an excess of PVL is present, it will often drag spores to the edge as it is flattened by the cover slip; better to use a minimal amount, then fill in vacant areas under the flattened cover slip by adding an excess of PVL from the side. If the spores are wet, the PVL sometimes becomes cloudy but will clear overnight. The slides are then allowed to dry and harden, a process which may take a week or more at room temperature but is hastened by keeping them on a warming table. PVL evaporates slowly even when solidified, so an initial excess at the edge of the cover slip is useful. Even so, gaps may appear under the cover slip during hardening and should be filled with fresh PVL. Once the mount is hardened and filled to the cover slip edge, seal with fingernail polish, porcelain cement, or a similarly impervious material. These slides will last indefinitely. Spores stained in cotton blue or Melzer's reagent can be similarly mounted in PVL, and the color reactions will be retained apparently indefinitely.

Data to accompany the herbarium-desposited specimens includes locality, date, and elevation of collection (or of original source of pot-cultured spores), associated hosts, history of pot culturing when applicable, color of spores and attached hyphae when fresh, and collectors' names. Other descriptive notes on the collection or photographs of the habitat or the specimens increase the value of the collection.

Any receptive public herbarium is suitable for deposit of collections of Endogonales. Normally the herbarium of the collectors' institution would be used. If the institution has no mycological herbarium, one option is the Oregon State University Mycological Herbarium, which has become a world depository for Endogonales. It also welcomes duplicates of collections placed in other herbaria.

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